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THE CONCRESCENCE THEORY OF THE VERTEBRATE EMBRYO.

BY CHARLES-SEDGWICK MINOT.

(Continued from page 516).

The Meroblastic Embryo.—Considerations of practical convenience have led to the custom of distinguishing in the development of meroblastic ova the embryonic from the extra-embryonic portions. The distinction is in reality entirely arbitrary, for the whole of the ovum is included, morphologically speaking, within the body of the embryo. Custom has led to designating the two parts as the embryo and the yolk; the student should be careful not to allow himself to be misled by these terms. In the laboratory it is a general practice to remove the so-called "embryo" from the yolk, and in doing this the entodermic cavity loses its inferior wall, to wit, the entodermic yolk. Let the relations be represented by the accompanying diagram, the embryo being drawn very much too large in proportion to the yolk for the sake of clearness. Suppose the layers to be cut through on the lines, *x x'*; we could then remove the embryonic portion. This is what is actually done in practice. It is very important to understand clearly that the yolk is part of the embryo, and that our sections usually represent only a torso.

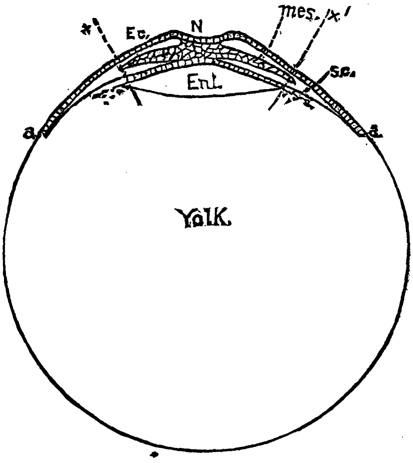

FIG. 10.—Diagram showing the relations of a vertebrate ovum with an embryo in cross-section and a large yolk. *Ec*, ectoderm; *N*, neural groove; *mes*, mesoderm, *s. c.*, segmentation cavity; *Ent*, archenteric cavity; *a*, *a*, ectodermal vein, where the ectoderm is growing over the yolk.

Structure of the primitive streak.—For our purposes it is convenient to give 1°, a general comparative account; 2°, a more detailed description of the mammalian ovum up to the stage with completed primitive streak.

1°. *Vertebrate primitive streak.*—It is advisable to begin with the consideration of the arrangement as we find it in eggs of marsipobranchs, ganoids, and amphibians, since these eggs are probably more primitive in their mode of development than those of other vertebrates. The points of most importance in my judgment are illustrated in Fig. 11, A and B. In A, we have a section through the middle portion of a partly-formed primitive streak of an axolotl, the streak still requiring considerable additions at its hinder end before attaining its full length; the archenteric cavity, *Ae*, is a large space bounded above by an epithelium, *en*, and below by the large mass of yolk-cells; the two-layered ectoderm, *Ec*, everywhere bounds the section; above the archenteron and below the ectoderm lies the accumulation of cells constituting the primitive streak, *pr;* the lateral prolongations, *Mes*, of the streak represent the commencing mesodermic outgrowths; whether the mesoderm grows out from the primitive streak, and

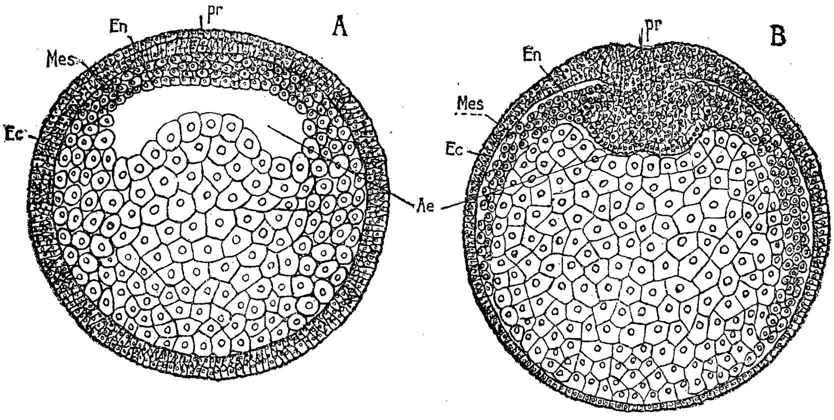

FIG. 11.—Sections of axolotl eggs: after Bellonci. *A*, frontal section somewhat anterior to the blastopore, from an egg in which the archenteron was partly formed, but the anus of Rusconi not delimiated. B, frontal section of an older ovum with well marked but large anus of Rusconi; the section passes just in front of the blastopore. *Ec*, ectoderm; *En*, entoderm; *Mes*, Mesoderm; *Ae*, archenteric cavity; *Pr*, primitive streak.

subsequently expands solely by its own proliferation, or whether it receives at its periphery accretions from the yolk-cells, is uncertain. I am inclined to think that the mesoderm does at first receive additions from the yolk. In B we have a similar section, but of an older stage, and through the hind end of the nearly full-grown streak; the general arrangement is the same as in A; we note the following differences: the primitive streak, *Pr*, is very thick, and composed of numerous small cells, and its lateral mesodermic expansions, *Mes*, extend further around the ovum. In both sections we see that the cells of the primitive streak are not marked off from those of the adjoining entoderm. In a longitudinal section, as is illustrated by that of a sturgeon, Fig. 7, *ante*, p. 510, we see that the mesoderm or tissue of the primitive streak runs way forward, and is thickest around the blastopore. The disposition of the parts and the appearance of the cells vary in the three groups we are considering, but for our purpose it is unnecessary to describe these secondary differences. The points essential to note are that the primitive streak is formed by mesoderm, which is accumulated along the line, and is thickest around the blastopore, and which spreads laterally between the ectoderm and entoderm; in the axial region the mesoderm is not separated from the entoderm; the blastopore passes through the thick hind end of the streak.

In elasmobranchs the differentiation of the axial tissues begins in the embryonic rim before concrescence takes place, so that while the type affords peculiarly conclusive evidence of concrescence, it is less convenient for the study of the primitive streak since the hind end of the primitive streak is, as it were, divided, being continued as the embryonic rim right and left. The degree of differentiation varies extremely; in Pristiurus the mesoderm grows out from the embryonic rim; in Scyllium the mesoderm grows out, and the differentiation of the notochord begins; in Torpedo (Rückert, *48*, 101) the myotomes appear in the embryonic rim before concrescence, as in Elacate among teleosts. The relations are further complicated by the advance in development of the axial structures while concrescence is going on, so that, as for instance in Pristiurus, Rabl, *44*, 116-129, the notochord may be differentiated while the mesoderm is still developing in the embryonic rim. The precocious changes in the embryonic rim demand especial attention when the origin of the mesoderm is discussed. The ectoderm, as soon as it becomes one-layered, consists of high cylinder cells. As development progresses the ectoderm thins out except at either side of the axial line. The mesoderm arises from the entoderm, close to the ectental line, and is there quite thick, but as it stretches away it thins out. Now, if it be remembered that the ectental lIne becomes the axial line when concrescence takes place it is evident that this mesodermic thickening of the entoderm is in reality axial thickening, and when concrescence takes place it fuses with the corresponding thickening of the opposite side and constitutes an actual axial thickening or true primitive streak; but in elasmobranchs as soon as the anterior axial structures have concresced we find by precocious development that the notochord and medullary groove appears; now, as I have shown elsewhere, the appearance of these structures causes the division of the axial mesoderm into completely separated right and left portions. It is only by keeping the process of concrescence and the precocious development of the parts constantly in mind that we can understand the development in elasmobranchs or compare it rightly with that of other types. From what has been said it is clear that a section of the blastodermic rim from which the mesoderm was just growing out would correspond to half a section of, say, a bird's ovum through the primitive streak, and upon comparison it will be found that all the essential relations are identical.

The structure of the primitive streak in birds has been repeatedly investigated and the subject of much discussion. As the observations of Duval, *17*, *18*, appear to me the most thorough, and as my own preparations have enabled me to confirm many of his statements, I follow in the main that author. Duval's statements have also been verified in many essential points by Zumstein, *69*. Other important authorities to be consulted are Kölliker in both his text-books; His *25*, *28*, *29*, etc.;

Koller, *31 ;* Disse, *15, 16 ;* Waldeyer, *64, 65 ;* M. Braun, *12 ;* Gasser, *21, 22 ;* Rauber, *46 ;* C. Rabl, *44*.

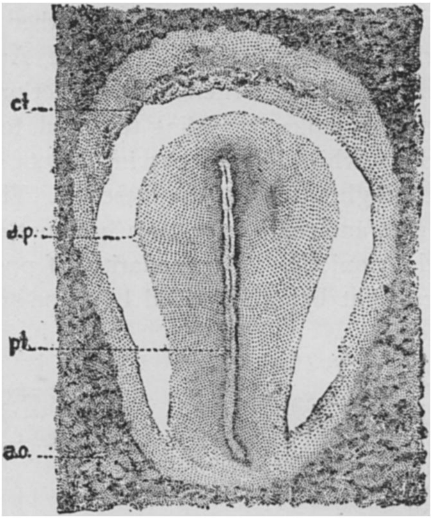

FIG. 12.—Area pellucida of a hen's egg with complete primitive furrow; after Duval. *Ao*, area opaca; *ct*, anterior crescent; *Ap*, area pellucida; *pt*, primitive groove. x 20 diam.

The following description applies to the hen's egg. When the egg is laid the centre of the segmented blasto-disc presents a circular area of lighter color; during the first few hours of incubation this *area pellucida*, as it is called, becomes more distinct; as concrescence goes on the *area pellucida* expands, and the primitive streak appears in it excentrically between the eighth and twelfth hour. By the sixteenth hour the primitive streak has its full length. The rate of development is extremely variable, autumn eggs developing more slowly than spring eggs; the eggs vary also individually, and are moreover much influenced by the temperature of their incubation. For a fuller discussion of these variations see His, *25*, 56–63. Seen from the surface the *area pellucida* with completed streak presents the following features: the *area pellucida, ap*, is considerably elongated and somewhat pear-shaped, being widest at the anterior end of the primitive groove, *pt;* this groove is well marked as a narrow and shallow furrow, which begins some distance from the anterior edge of the area, and ends just before reaching the posterior edge of the area; the front end of the furrow usually bends slightly to the left, but not invariably, as Koller and Rabl have maintained, for it sometimes bends to the right or is quite straight; a line of granules is sometimes noticeable above the primitive groove; they were seen by Dursy, *l. c.*, and are called by Duval, *17*, p. 15, the *filament épiaxial*, compare Gasser, *14*. The portion of the *area pellucida* immediately around the primitive groove appears slightly darker than the rest. The anterior portion of the pellucida is further distinguished by the anterior crescent, *ct*, the "vordere Aussenfalte" of His, *25*, and other German writers. The anterior crescent is a temporary appearance due, according to Duval, to a series of folds of the entoderm, which forms a curving row of shallow pockets, that, shining through, mark out the crescent. The crescent disappears a little later, and there arises, nearly if not quite in its place, a new fold, the amniotic. The similarity of position has led to the anterior crescent being identified by some authors with the true amniotic fold.

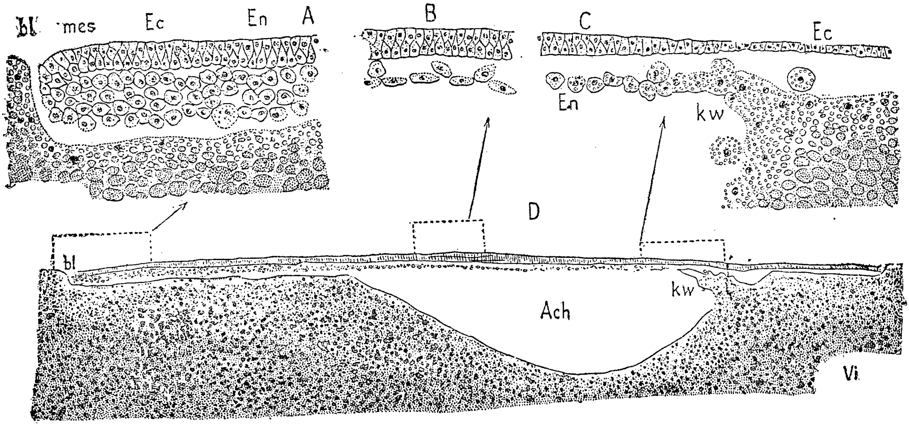

FIG. 13.—Longitudinal section of the region of the primitive streak of a hen's ovum incubated six hours; after Duval. *D*, general view magnified about 40 diameters; *A*, *B*, *C*, details of *D*, with higher magnification; *Ec*, ectoderm; *Mes*, mesoderm; *Ent*, entoderm; *bl*, blastopore; *k w*, germinal wall (keim wall); *Ach*, archenteric cavity.

Longitudinal and transverse sections are very instructive. We begin with the examination of a *longitudinal section* of a somewhat younger stage, in which the blastopore is open. Later the ectoderm closes behind the primitive streak, as already stated, and spreads backward over the yolk. The section shows that the yolk is not divided into cells, although nuclei are scattered through it; the nuclei are represented as black dots in *A* and *C*. The cavity of the archenteron, *Ach*, is enlarged by the formation of a deep pit in the yolk, while the posterior half of the cavity remains a narrow fissure between the cellular entoderm, *Ent*, and the yolk; the archenteron communicates with the exterior by the blastopore, *bl.* The entoderm is a loosely put together stratum of cells, which passes over anteriorly into a ridge of the yolk in which cells are being produced around the already accumulated nuclei; this ridge, *k w*, is the germinal wall. Posteriorly the cell layers are much thicker, *A;* the ectoderm is clearly differentiated from the underlying cells, which are all more or less alike, though they represent both the entoderm and mesoderm. From this connection and from the fact that the connection between the ectoderm and mesoderm, which is so well known to exist after the primitive streak has attained its full length, Duval concludes that the mesoderm arises primitively from the entoderm. *Transverse sections* afford additional information. The accompanying figure, 14, represents cross sections of a germinal area the primitive streak of which has attained about one-half its full length. The first section, Fig. 14, *A*, passes through the anterior region of the area pellucida; it shows the large cavern, *Ach*, of the archenteron hollowed out in the yolk; the entoderm, *Ent*, above the cavity is a thin layer of cells, connected laterally with a projecting shelf of yolk, *k w* (the *bourrelet entodermo-vitellin* of Duval), which is rich in nuclei, and subse-

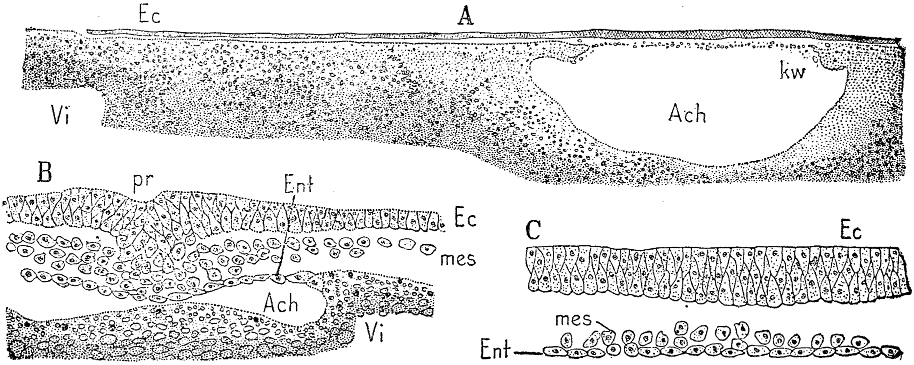

FIG. 14.—Transverse sections of a germinative area with half formed primitive streak; after Duval. *A*, through the anterior region of the area pellucida; *B*, through the primitive streak; *C*, part of *A* enlarged; *Ec*, ectoderm; *Mes*, mesoderm; *Ent*, entoderm; *k w*, germinal wall (Keimwall); *Ach*, archenteric cavity; *Pr*, primitive groove; *Vi*, yolk.

quently expands very far and acquires a more cellular character; this shelf is the commencement, therefore, of the *Keimwall* of German writers. Immediately above the entoderm and intimately connected with it are a few cells which belong to the mesoderm, *C*, *Mes;* the ectoderm is quite thick, *C*, *Ec*, and consists of high columnar cells; towards its periphery the ectoderm thins out, and its edge rests upon the yolk, with which it has no connection. In the region of the primitive streak, Fig. 14, *B*, the fundamental relations are the same, but there are important differences to note. The entodermic cavity, *Ach*, is very much smaller; the mesoderm is much thicker, and in the axial region fuses with both the ectoderm and entoderm, thus forming the *Achsenstrang* (axial cord) of German writers; the mesoderm also spreads out over the yolk far beyond the archenteric cavity, about one-third of the way from the axial line to the distal edge of the ectoderm; the ectoderm is disposed about as in the previous section, except that in the centre it merges into the mesoderm and presents externally a small notch corresponding to the section of the primitive groove. There appears to me no satisfactory evidence that the mesoderm receives, as some writers have maintained, peripheral additions from the yolk. In both sections the yolk under the blastoderm contains numerous nuclei near its surface.

Modifications very soon ensue in the Sauropsida (birds and reptiles) by which the disposition of the mesoderm is considerably changed, especially in three respects, namely: by the appearance of the so-called head process (Kopffortsatz), by the axial connection of the mesoderm with the ectoderm, and by its losing in part its connection with the mesoderm. During these changes the archenteron expands rapidly, the archenteron expands rapidly, the entoderm becomes very thin in the region of the are apellucida, and passes more and more abruptly, as development progresses, into the so-called germinal wall of the area opaca; finally the ectoderm becomes thinner peripherally; so that the axial thicker part is gradually marked off more and more abruptly. Sections of a stage with a primitive groove at its maximum,—a stage which is usually found towards the end of the first day of incubation,—show three changes clearly. A cross section through the area opaca in front of the area pellucida shows the thin ectoderm, the thick cellular entoderm overlying the archenteric cavity and charged with yolk granules; the entodermic nuclei are very variable in form and irregular in distribution; the cell boundaries are indistinct. There is no mesoderm. A cross section near the front of the area pellucida likewise shows only ectoderm and entoderm; the former is a high cylinder epithelium over the area pellucida and thins out towards the opaca on each side; the latter is a thin layer over the area pellucida, and passes quickly but not abruptly into the very thick yolk-bearing entoderm (or Keimwall) of the area opaca. Sections a short distance in front of the primitive groove show that the head process (*Kopffortsatz*) is a forward prolongation of the primitive streak and consists of an axial accumulation of the mesodermic cells, fused with the entoderm, and having broad extensions sideways to form the mesoderm beeween the outer and inner germ-layers; the lateral portions of the mesoderm have no connection with the outer germ-layers, and at its distal edge the mesoderm thins out and rests upon the entoderm of the opaca, but without being connected with it; I cannot find any satisfactory evidence that it receives any additions from the opaca entoderm, as many authors have maintained. The ectoderm in the region of the Kopffortsatz resembles that further forward, but it very soon shows a faint median furrow, the so-called dorsal groove (*Rückenrinne*), which is the commencement of the medullary groove. In the anterior half of the primitive streak the relations are similar to those in the head process, ex-

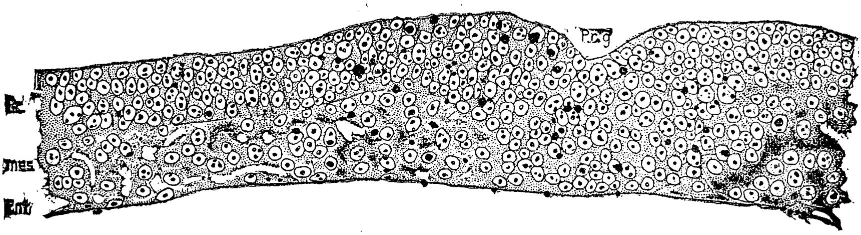

FIG. 15.—Transverse section of the anterior region of a fully developed primitive streak of a hen's ovum. *Ec*, ectoderm; *mes*, mesoderm; *Ent*, entoderm; *Pr.g*, primitive groove. The black dots represent yolk granules.

cept that the ectoderm shows the primitive groove, Fig. 15, and is fused with the axial cord (*Achsenstrang*) of the mesoderm, so that in the axial region the three layers are united. In the posterior region of the primitive groove the connection of the mesoderm with the inner germ layer is dissolved, but the connection with the entoderm is retained. Behind the primitive groove the mesoderm extends, but lies free between the ectoderm and entoderm. To recapitulate:—There is a long axial mesodermic thickening, which has the primitive groove over its posterior two-thirds; the thickening in front of the groove is united with the entoderm and is called the head process; the thickening under the front half of the groove is united with both the ectoderm and entoderm; the thickening under the hind half of the groove is united only with the entoderm; it is to be remembered that the mesoderm arises from the entoderm, and its connection with the ectoderm is, it seems to me, to be considered secondary.

A comparative examination of the primitive streak, as described for various classes in the preceding pages, shows that it has a remarkable uniformity of organization. In all types it consists of an axial accumulation of mesodermic cells; this mesodermal axial cord overlies the archenteron, and sends out mesodermic tissue in a widening sheet between the ectoderm and entoderm, headwards, sideways, and backwards; the mesoderm is thickest posteriorly, *i. e.*, in the region of the blastopore; when it first appears it is intimately connected with the entoderm except in the neighborhood of the blastopore, where both entoderm and mesoderm unite with ectoderm. The mesoderm constitutes an axial mass, and offers no trace of a bilateral division or origin. Such a division is produced secondarily by the meeting of the medullary and notochordal grooves. The ectoderm in the region of the primitive streak consists of high cylinder cells, but it gradually thins out toward the embryonic rim. The entoderm on the dorsal side of the archenteron consists of discrete cells, which soon acquire a distinctly epithelial arrangement; laterally and in front it passes over into the yolk, which may be cellular or a multinucleate mass. These features recur in all the types we have studied, though the variations are very great. In the immediately following stages there is a rapid expansion of the mesoderm, in all directions, and also an expansion of the archenteric cavity, which is especially noticeable in meroblastic ova. The relations of the blastopore are discussed below.

2°. *Mammalian primitive streak.*—The description of the primitive streak has to be preceded by an account of the changes in the blastodermic vesicle from the close of segmentation to the appearance of the primitive streak.

Mammalian blastodermic vesicle.—After the close of segmentation we find that the inner mass becomes flattened out, and in the region it occupies we can distinguish three layers of cells, as previously described, *first*, counting from the outside the thin layer of cells known as Rauber's "Deckschicht;" *second*, a middle layer of cylindrical cells, which becomes the ectoderm; *third*, an inmost layer of thin flattened cells, which belong to the entoderm; the "Deckschicht" continues round the whole vesicle as a single layer; the others layers do not so continue.

The next step in development is the formation of a second layer which spreads out in all directions from the region of the inner mass; hence as far as the new layer reaches the blastodermic vesicle becomes two-layered. Meanwhile the "Deckschicht" disappears, leaving two layers in the region of the inner mass; it is to be remarked that the "Deckschicht" is retained in certain rodents, undergoing special modification as described in the section on inversion of the germ-layers. The stage in which the vesicle is partly two-layered, while the "Deckschicht" is still present, is exemplified in Fig. 16.

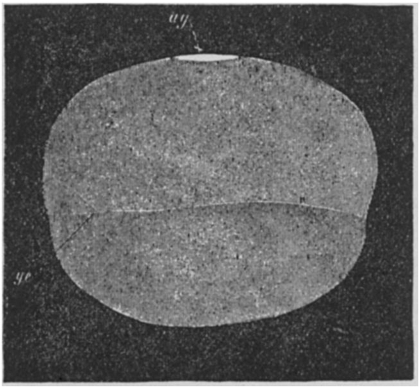

FIG. 16.—Blastodermic vesicle of a rabbit of seven days. *ag*, area germinativa or embryonic shield; *ge*, line, above which the vesicle is two layered.

Blastocyst of the rabbit of six days.—The development is exceedingly variable, so that exact times cannot be given. The general appearance is illustrated by Fig. 16. from Kölliker. The vesicle figured was 4.4 mm. in length; the envelopes of the ovum are not shown, though they were still present; at the upper pole is the small embryonic shield, corresponding in position to the inner mass; it is marked out by the greater thickness of the walls of the vesicle; the developing second layer extends over more than half the vesicle, reaching to the line *ge*.

The following is a summary of Ed. van Beneden's description, *2*, 185-200, of the blastodermic vesicle of a rabbit at 6 days, 1½ hours after coitus. The vesicle measured 3.2 mm. in diameter; it was nearly spherical; the wall of one hemisphere consisted of one layer of cells; the other hemisphere had two layers of cells, and besides in its central portion a third layer intervening between the other two. The area with three layers van Beneden designates as the *tache embryonnaire;* it showed no trace of the primitive streak; it was oval in outline, and had one point, which the author identifies as Hensen's knot, where the layers adhere together closely. Transverse sections show that the outermost layer of cells is a low cylinder epithelium, which at the edge of the area passes into a thin epithelium quite abruptly; it corresponds to Rauber's "*Deckschicht*," and has been said by him to flatten out and disappear, leaving the cells underneath as the outer layer of the embryonic vesicle in later stages, compare the following paragraph. The cells of the innermost layer are thin and wide; they are called the hypoblast (entoderm) by van Beneden; the cells themselves have round nuclei, around each of which is accumulated a court of granular protoplasm; the adjacent courts are connected by a coarse meshwork of protoplasmic threads; treatment with nitrate of silver brings out the cell boundaries, and divides the reticulum into polygonal areas. The cells of the present outermost layer have distinct boundaries and contain granules, and long bacilliform bodies, which van Beneden saw also in the fresh specimens, and found to be constant appearances. Similar bodies are found in the germinal vesicles of sheep, and are held by Bonnet, *10*, to be derived from the uterine milk; the rabbit is not known to have uterine milk. The histological peculiarities of these two layers remain about the same from the fifth to the eighth day. The middle layer consists of rounded cells with numerous granules; seen from the surface their diameter is greater than that of the cells outside them, but much less than that of the cells underlying them. While we know that the middle layers are ectodermal, it is uncertain whether the inner layer is really entodermal or really belongs with the two outer layers as part of the primitive blastoderm or ectoderm; in the latter case, the true entoderm of the archenteron must arise later, as we must consider probable also for the reason that the primitive streak is not yet formed.

HISTORY OF GARDEN VEGETABLES.

BY E. L. STURTEVANT.

(Continued from p. 332.)

ROCKET SALAD. *Brassica eruca* L.

THIS strong and to most persons offensive plant has been long under culture, and is even now highly esteemed by the Greeks and Turks, who prefer it to any other salad.[1] It was cultivated by the ancient Romans. Albertus Magnus[2] in the thirteenth century speaks of it in gardens; so also does Ruellius[3] in 1536, who uses nearly the present French name, *roqueta*. In 1586 Camerarius[4] says it is planted most abundantly in gardens. In 1726 Townsend[5] says it is not now very common in English gardens, and in 1807 Miller's Dictionary[6] says it has been long rejected. It was in American gardens in 1854 or earlier,[7] and is yet included by Vilmorin[8] among European vegetables.

[1] Walsh. Hort. Trans., VI., 53.
[2] Albertus Magnus. De Veg., Jessen Ed., 1867, 507.
[3] Ruellius. De Nat. Stirp., 1536, 513.
[4] Camerarius. Epit., 1586, 306.
[5] Townsend. Seedsman, 1726, 18.
[6] Miller's Dict., 1807.
[7] Brown. Pat. Off. Rept., 1854.
[8] Vilmorin. Les Pl. Pot., 1883, 541.